Success of spatial statistics in determining underlying process in simulated plant communities

Success of spatial statistics in determining underlying process in simulated plant communities

Spatial statistics in simulated plant communities

Authors:

Calum Brown[1*], Janine B Illian[2,3] and David F R P Burslem[4]

1University of Edinburgh, School of Geosciences, Geography Building, Drummond Street, Edinburgh EH8 9XP.

2University of St Andrews, Centre for Research into Ecological and Environmental Modelling, Buchanan Gardens, St Andrews KY16 9LZ

3Department of Mathematical Sciences, Norwegian University of Science and Technology, 7491 Trondheim, Norway.

4University of Aberdeen, School of Biological Sciences, Cruickshank Building, St Machar Drive, Aberdeen AB24 3UU

*Correspondence author. Email: calum.brown@ed.ac.uk,

Summary

1. Spatial statistics are widely used in studies of ecological processes in plant communities, especially to provide evidence of neutral or non-neutral mechanisms that might support species coexistence. The contribution of such statistics has been substantial, but their ability to identify any links between underlying processes and emergent patterns is not certain.

2. We investigate the ability of a number of spatial statistics to distinguish theorised mechanisms of species coexistence (spatial and temporal niche differentiation, neutrality, the Janzen-Connell effect and heteromyopia) in a simulated plant community.

3. We find that individual statistics differ substantially in their sensitivity to these mechanisms, with those based on nearest-neighbour species identities being the most sensitive. These differences are largely robust to changes in the strength of the modelled mechanisms when simulated independently and in combination. The spatial signal of niche differentiation is always distinct in simulations that combine mechanisms.

4. Synthesis. We describe full spatial signals of modelled coexistence mechanisms that are observed consistently across statistics and simulated strengths and combinations of mechanisms, and identify a set of spatial statistics that holds particular promise for empirical studies designed to investigate mechanisms of these kinds.

Key-words: coexistence mechanisms, determinants of plant community diversity and structure, environmental niche, heteromyopia, ISAR, Janzen Connell, lottery model, neutral theory, point pattern, spatial Simpson index.

Introduction

Statistics that summarise spatial relationships among individuals are of considerable value in ecology, where many processes influence, and are influenced by, spatial structure (Watt 1947; Law *et al*. 2009). These processes include niche differentiation (Wang *et al.* 2011), positive and negative interactions among species (Stoll & Prati 2001), density dependence within species (Clark & Clark 1984; Packer & Clay 2000), and dispersal limitation (Seidler & Plotkin 2006). All of these processes, alone or in combination, are thought to play a substantial role in the dynamics of plant communities, and their detection and quantification is a major aim of forest ecology in particular.

Of special interest are processes that might enable very large numbers of species to coexist in tropical rainforests (Wright 2002). The long-running debate over the identity of these processes has been given fresh impetus in recent years by findings that the observed non-spatial characteristics of tropical tree communities (such as species diversity or abundances) are described well by neutral models that assume ecological equivalence among species (Hubbell 2001; Bell 2001). Attempts to ascertain the role of neutral dynamics, as opposed to the more established niche differentiation (Grinnell 1917; Hutchinson 1958) or Janzen-Connell effects (Janzen 1970; Connell 1970) have been manifold (e.g. Hardy & Sonké 2004; Ruokolainen *et al.* 2009; Tang & Zhou 2011; Gueze *et al.* 2013; Chase 2014). Popular summaries of species occurrence, diversity or abundances have failed to provide a resolution (e.g. Hubbell 2001; Chave 2004; McGill *et al.* 2007), but summaries of spatial structure have a rich potential to contribute to this debate (Condit *et al.* 2000; Brown *et al.* 2011; 2013; Baldeck *et al.* 2013; Bar-Massada *et al.* 2014).

Many studies of spatial structure have focused on variations in diversity, often using measures of β-diversity that summarise some aspect of the turnover in species composition with site (e.g. Jaccard 1912; Odum 1950; Shimatani 2001; Legendre *et al*. 2005; Anderson *et al.* 2011; Gonzalez-Caro *et al.* 2014). However, the majority of spatial statistics used in ecology describe intra- or inter-specific clustering. Spatial point process theory, which provides statistical models and descriptions of patterns formed by individuals in space, has become increasingly important as a basis for analyses of point patterns (Matérn, 1960; Stoyan & Penttinen 2000; Illian *et al.* 2008; Wiegand & Moloney 2014). Ripley's K-function and its non-cumulative equivalent, the pair correlation function, have been particularly widely used (e.g. Salonen *et al.* 1992; Hardy & Sonké 2004; Wiegand *et al.* 2007b).

Spatial statistics have often proved useful in identifying the signals of particular ecological processes in the relative locations of tree species (Mladenoff *et al*. 1993; Law *et al.* 2009; Wang *et al*. 2010), or in studying associations and interactions among species (Wiegand *et al.* 2007b; Martinez *et al.* 2010; Zhang *et al.* 2010; Wang *et al.* 2011). Several recent studies suggest that spatial structure may indeed be used to distinguish neutral and non-neutral processes (Münkemüller *et al.* 2012; Brown *et al.* 2013; Baldeck *et al.* 2013; Bar-Massada *et al.* 2014; May *et al.* 2015). Dispersal limitation and niche differentiation have both been frequently investigated through their spatial effects (e.g. Smith & Lundholm 2010; Wang *et al*. 2010; Lin *et al.* 2011; Beaudrot *et al.* 2013). Nevertheless, patterns generated by environmental variation and limited dispersal remain difficult to distinguish (Wiegand *et al* 2007a; Kraan *et al.* 2010), although new techniques for spatial point process modelling offer promise for separating the effects of these processes (e.g. Illian *et al.* 2012; Jalilian *et al.* 2013).

84 The wide range of applications for spatial statistics in forest ecology has led to a
85 proliferation of statistics that are based on similar or identical spatial information. However,
86 reviews of the relative abilities of different spatial statistics to describe patterns of interest
87 have been scarce (Dale *et al.* 2002; Tuomisto 2010; Anderson *et al.* 2011; Wiegand *et al.*
88 2013), and the relationships among them have not been formally assessed. Furthermore,
89 there have been few theoretical investigations of the implications of proposed coexistence
90 mechanisms for spatial structure (but see e.g. May *et al.* 2015). As a result, neither the
91 spatial signals of important processes nor the abilities of spatial statistics to detect them are
92 fully understood, hindering attempts to investigate the dynamics of real-world
93 communities.

94 Here, we carry out a comprehensive assessment of the sensitivity of a number of different
95 statistics to five theorised mechanisms of species coexistence in plant communities: neutral
96 dynamics (Hubbell 2001), spatial niche differentiation, temporal niche differentiation, the
97 Janzen-Connell effect, and heteromyopia (Murrell & Law 2003). In order to do so, we
98 isolate the signals of these mechanisms by running stochastic simulations of forest
99 communities under the basic assumptions of each mechanism separately and in
100 combination. Our primary aim is to investigate the sensitivity of different statistics to the
101 modelled mechanisms, whether they operate alone or together. This is expected to
102 represent a first step in the development of empirically testable predictions of spatial
103 structure that differ among theorised coexistence mechanisms.

104 A secondary aim is to fully characterise the spatial signals of the mechanisms that we model,
105 in order to assess potential links between underlying processes and observed patterns.
106 Spatial structure is complex and includes a number of distinct characteristics, such as the

magnitude and spatial scale of associations among individuals of the same and different species. Any one statistic is therefore unlikely to capture the full spatial signal of a particular mechanism and, being a summary of spatial structure, may discard some relevant information (e.g. Wiegand *et al.* 2013). We distinguish spatial statistics according to whether they describe within- or between-species structure (Fig. 1), at what level (species or community) they operate, and further identify the individual items of information that comprise them. In this way, we can determine precisely those characteristics of spatial patterns that the modelled mechanisms affect, and whether these are most clearly discernible within or between species. This finally enables us to propose an informative combination of existing spatial statistics that together capture the principal spatial consequences of each simulated mechanism, and therefore may provide additional information for empirical studies of underlying processes in plant communities.

Materials & Methods

SPATIAL STATISTICS

We do not attempt a comprehensive review of published spatial statistics, but instead concentrate on a small number that are particularly representative (selected according to the information that they use and their prior application in relevant studies). We divided statistics into those that describe within-species spatial structure and those that describe between-species spatial structure (bivariate or multivariate). All are sensitive to some form of attraction or repulsion among individuals, where independent spatial distributions indicate a lack of interaction (Wiegand & Moloney 2004). Within-species patterns vary

between clustering and regularity of conspecifics, while between-species patterns vary between mingling and segregation of heterospecifics (Fig. 1).

We considered three statistics describing within-species structure and four describing between-species structure (these are summarised in Tables 1 and 2). Together, these statistics employ the principal spatial and non-spatial pieces of information available for the construction of statistics in plant community ecology (Table 1), and so allowed us to draw broad conclusions about the ability of groups of spatial statistics to detect the processes that we model.

The three measures describing within-species spatial structure that we considered were the degree of aggregation (Coomes *et al.* 1999), the measure of interspecific segregation (Dixon 1994, which despite its name describes the spatial structure of conspecifics); and the proportion of conspecific neighbours (e.g. Wiegand *et al*. 2007a) (Table 2). The four measures describing between-species spatial structure that we considered were the individual species-area relationship (ISAR) (Wiegand *et al.* 2007a; which captures similar information to the Species Area Relationship), the spatial Simpson index (Shimatani 2001; Rajala & Illian 2012), the degree of association (Coomes *et al.* 1999) and the cross-pair overlap distribution (xPOD) (Brown *et al.* 2011). All of these measures vary in their sensitivities to spatial scale and community size and diversity (Table 2), and several are closely related or equivalent to spatial point process functions such as Ripley's K (Table S4).

The ability of the xPOD to distinguish the coexistence mechanisms modelled here has been established previously (Brown *et al.* 2011), and the degree of association is expected to be similarly sensitive due to the information it shares with the xPOD. The spatial Simpson index and the ISAR are sensitive to species richness or abundances, and the mechanisms we

model have no clear *a priori* consequences for these. Nevertheless, these measures do allow for the comparison of signals in spatial patterns with those in diversity or abundances. Each statistic was calculated at species level (Table 2) and community level (Table S5), where the ISAR was further normalised by species richness (the spatial Simpson index was not normalised by relative abundances because it would then contain only the information already captured by other statistics).

ECOLOGICAL SIMULATIONS

In order to test the sensitivity of the eight spatial measures to particular ecological processes, we used data from a large set of new simulations of a model presented in Brown *et al.* (2011). These were replicated simulations from a stochastic individual-based model of a species-rich plant community in continuous toroidal space, in which multispecies spatial patterns were allowed to develop through several million birth and death events. These events occurred according to the individual and combined assumptions of neutral, niche, lottery (temporal niche), Janzen-Connell or heteromyopia mechanisms, which were chosen as the principal theorised mechanisms of species coexistence in diverse plant communities. This approach allowed any spatial signals of these modelled mechanisms to be isolated from any potentially confounding effects and assessed.

Under neutrality, the only processes included were density-dependent mortality, dispersal limitation (both of which occurred identically in all species) and the immigration of new species. These processes also occurred in the other simulations but were adjusted as follows: in the niche simulations, individuals had lower death rates when they were within their species' preferred environment (within a geographically defined, continuous and symmetrical environmental gradient; Brown *et a;.* 2011 Fig. 1(d)); in the lottery simulations,

all species' death rates varied at random time intervals to represent the effects of environmental changes; in the Janzen-Connell simulations local density-dependent mortality took a higher value within species than between them; and in the heteromyopia simulations density-dependent mortality occurred over larger areas within species than between them. Parameterisations of each set of simulations are given in Table S1, and complete descriptions of each model are provided in Brown *et al.* (2011) (the only modifications being to improve simulation speed and the representation of bivariate Gaussian dispersal kernels).

As in Brown *et al.* (2011), these simulations are intended to provide evidence of the fundamental spatial properties of the modelled processes (alone and in combination). Direct relevance to real-world communities, where many different processes occur and interact at a range of species-specific strengths, is inevitably limited. Nevertheless, conclusions drawn in these and other simulated settings have empirical value, in generating testable hypotheses concerning real-world spatial structure, developing and comparing spatial statistics, and in improving understanding of the modelled processes (Gravel *et al.* 2006; Brown *et al.* 2011; 2013; Flügge *et al.* 2012).

Thirty realisations of each mechanism were generated so that the variability in the properties of the resulting spatial patterns could be assessed, and the spatial measures defined in Table 2 were calculated for each realisation (parameterisations were consistent across realisations). We then randomly re-assigned species identities (while preserving abundances) across individuals in each of the simulations and re-calculated the spatial measures, to check for spatial effects of model design unrelated to the mechanisms being modelled. We also varied the strength of each modelled mechanism over an additional forty realisations (ten per non-neutral mechanism, from nearly neutral to strongly non-neutral;

198 Table S2) in order to assess changes in the sensitivity of the statistics used to the modelled
199 mechanism. Finally, we ran another twenty-five simulations in which mechanisms were
200 pairwise combined at each of three defined strengths (Table S3) to investigate the
201 robustness of the spatial characteristics identified from the preceding, single-mechanism
202 simulations.

203 COMPARING SPATIAL STATISTICS

204 Statistics describing spatial structure were compared on the basis of their ability to
205 distinguish the mechanisms described above using their resulting modelled spatial patterns.
206 For every simulated species across the 365 simulations and permutations, all statistics that
207 could give species-specific values were calculated on the torus and plotted. Subsequently,
208 all statistics were calculated for each simulated community (realisation) of each modelled
209 mechanism. Some statistics, being scale-independent, gave single values in each case, while
210 others, being functions of distance, gave a range of values calculated at different scales
211 (Table 2). Statistics of the latter type were calculated to a maximum radius of one quarter of
212 minimum plot dimension (0.25 units) following the recommendation of Baddeley & Turner
213 (2005). Depending on observed sensitivity to spatial scale, statistics were calculated at
214 increments of radius of either 30 or 100 (increments of 0.0083 and 0.0025 respectively). In
215 this way, we were able to compare the abilities of the different statistics to distinguish the
216 modelled mechanisms by their effects on the patterns of individual species or entire
217 communities, and how these abilities varied with spatial scale.

218 The ability of each statistic to discriminate among the mechanisms of community assembly
219 was initially visually assessed on the basis of all simulation results (e.g. Fig 3(a)). For scale-
220 dependent measures, information from the radius or radii at which differences among the

mechanisms appeared greatest was used to construct boxplots of results; scale-independent measures were summarised immediately as boxplots (e.g. Figs. 2(b) & 3(b)). The overlap of these boxplots was again assessed visually, and distributions of values plotted for the radius at which overlap was minimised (e.g. Fig. S3). These distributions were finally characterised by their first three moments – mean, standard deviation and skewness (e.g. Table S6). We did not formally measure differences between results of different models as any such measure would be a function of arbitrary parameter settings rather than of fundamental differences between modelled mechanisms. Instead, we use the additional permutations and simulations described above to compare our results to those generated by random reassignment of species identities, and to conduct a sensitivity analysis to assess the robustness of our findings to variations in the strength of the modelled mechanisms in isolation and in pairwise combinations.

Having identified the measures that were most successful in distinguishing the modelled mechanisms, we combined those based on different information (Table 1) into a single plot intended to capture the principal spatial characteristics of the mechanisms. We then analysed the behaviour of this combination, including its sensitivity to variations in parameter settings, and investigated its ability to distinguish the modelled mechanisms in their general forms using principal component analysis. We present graphical results for the measures that best distinguish the different simulated ecological mechanisms here, and the remaining results in the Supporting Information. The results are based on species with an abundance of at least 100 individuals, because species of low abundance introduce a large amount of random variation and mask the signals from the modelled mechanisms.

Results

Within-species structure

Measures of within-species structure detected a number of differences between modelled mechanisms. These differences were generally not apparent in species-level results (the proportion of conspecific neighbours was most successful at this level; Figs. S2-3) but became clear when these results were averaged to community level. The degree of aggregation distinguished the niche, Janzen-Connell/lottery and neutral/heteromyopia results (Fig. S1), while the measure of interspecific segregation and proportion of conspecific neighbours gave distinct values for all but the neutral and heteromyopia results (Figs. 2 & 3). The proportion of conspecific neighbours was slightly higher under heteromyopia than neutrality at small spatial scales, but all measures suggested that total species clustering was minimised in the lottery simulations and increased through the Janzen-Connell, heteromyopia, neutral and finally niche simulations.

Between-species structure

Measures of between-species structure differed widely in their sensitivities to modelled mechanisms but again performed best when expressed at community level (species level results are presented in Figs. S4-S6). The (scale-insensitive) xPOD distinguished the niche mechanism, with a low mean and large variance in values compared to other mechanisms. Differences between the other mechanisms were limited, being restricted to some increase in mean values through the niche, heteromyopia, neutral, lottery and Janzen-Connell simulations, and some differences in the skews of the distributions. (Fig. S4 & Table S7). The ISAR (normalised to species richness; Table S7) performed considerably better, showing

substantial differences between the Janzen-Connell, neutral and heteromyopia simulations at small scales and complete separation between these, the niche and the lottery results (Fig. 4). A decreasing proportion of community diversity was found within local neighbourhoods across the lottery, Janzen-Connell, neutral, heteromyopia and niche mechanisms. The degree of association produced similar results, suggesting that species associations were strongest under the Janzen-Connell mechanism but decreasing in the same order otherwise. The spatial Simpson index, finally, completely distinguished all but the neutral and heteromyopia results at small radii (Fig. 5). The lottery mechanism produced the lowest values of the index at all radii, with the niche, neutral, heteromyopia and Janzen-Connell mechanisms giving increasing values.

Sensitivity analysis and combination of measures

These results allowed us to identify the measures that were most effective at discriminating among the mechanisms we modelled. This was achieved most successfully at the community level in all cases, where confounding variation between species had been averaged out (differences in this interspecific variation among mechanisms were not found to be as informative as the mean measures themselves). However, while species-level results from each mechanism were found to overlap to some extent, differences remained substantial enough to provide some discrimination of underlying mechanism.

Of the measures of within-species spatial structure, the proportion of conspecific neighbours was superior, being able to distinguish all mechanisms at community level with limited overlap only between the neutral and heteromyopia results (Fig. 3). Two measures of exposure were particularly successful: the ISAR (expressed as proportions of total species numbers in each simulation) and the spatial Simpson index. These could both distinguish all

289 but the neutral and heteromyopia mechanisms, and found some differences even between
290 these. The measures are also complementary to one another, because the ISAR uses only
291 local counts of species, whereas the spatial Simpson index uses individual neighbour counts
292 and 'global' species counts (relative abundances; Table 2). They therefore draw on distinct
293 information from a range of spatial scales, and detect slightly different characteristics of the
294 modelled patterns, as evidenced by the dramatic difference in the relationship between the
295 niche and lottery mechanisms as described by each (see also May *et al.* 2015).

296 Having identified these three measures as particularly informative, we graphically combined
297 them (using values from the most informative radii, where appropriate; see Fig. 6) in order
298 to illustrate all of the detected differences between modelled mechanisms in a single
299 summary (Fig. 6a). This showed clear separation between all mechanisms, and the results
300 of the sensitivity analysis, when expressed in terms of the same statistics, showed that this
301 separation was robust to the strength of the modelled mechanisms, with only the most
302 nearly neutral simulations producing similar results to one another (Fig. 6b). Mechanisms
303 either formed distinct groups or followed clear trajectories in 3-dimensional statistical
304 space, diverging in different directions as the strength of each modelled mechanism
305 increased.

306 These differences were also largely robust to different combinations of mechanisms at
307 different strengths (Table S3, Fig. 6c). This was especially true of simulations including the
308 niche mechanism, which always produced highly distinct results similar to those produced
309 by the niche mechanism alone, although the addition of the Janzen-Connell effect reduced
310 the strength of the niche signal in the spatial Simpson and proportion of conspecific
311 neighbours indices. The Janzen-Connell mechanism also eroded the distinction between
312 lottery and other results when used in combination. Of the three measures included in this

313 combination, the ISAR appeared to retain the greatest sensitivity to modelled processes,
314 with only the Janzen-Connell – heteromyopia combinations producing values consistent
315 with neutrality (though further work is required to test the reliability of these findings, as
316 some differences were small and potentially influenced by a lack of common species in
317 certain simulations).
318 Finally, results from randomisation of species identities expressed in terms of this
319 combination of indices show the almost complete loss of differences between simulated
320 mechanisms (especially for the proportion of conspecific neighbours) (Fig. S7). This suggests
321 that earlier findings are also robust to permutations of this kind, and therefore reflect
322 genuine spatial signals of the modelled processes rather than differences in species
323 abundances or experimental design. The exception is the lottery model, where spatial
324 Simpson and ISAR values approach those from the original simulations, implying that the
325 occurrence of a small number of (relatively) hyper-abundant species in the lottery
326 simulations means that measures which take account of overall diversity are sensitive to the
327 mechanism even where accurate spatial information is lost.

328 Further analysis of the combination of spatial statistics revealed that, for the initial 30
329 realisations of each modelled mechanism, the ISAR and proportion of conspecific
330 neighbours were strongly negatively correlated (having a Pearson correlation coefficient of -
331 0.989). Although the two measures are not directly dependent and could in theory respond
332 very differently to patterns (for instance the proportion of conspecific neighbours would not
333 distinguish between a high density of neighbours belonging to a single other species and a
334 high density belonging to several other species, while the ISAR would, but similarities would
335 increase as proportions of conspecific neighbours increase; Wiegand *et al.* 2007a), they
336 were not both necessary to distinguish mechanisms as modelled here. A principal

components analysis confirmed this, showing that the first two principal components, which placed very little weight on the ISAR, explained more than 0.9998 of variation in the results (Table S10). A plot of the first two principal components showed that the first alone was sufficient to detect most of the differences among the mechanisms, while the second was required to separate the niche/lottery and neutral/heteromyopia mechanisms (Fig 8). Given their respective make up, this implies that the spatial Simpson index, as a measure of between-species structure, can separate mechanisms that are or are not based on spatial or temporal niche differentiation, but that the proportion of conspecific neighbours, a measure of within-species structure, is necessary to distinguish between the effects of temporal and spatial niches.

Discussion

In recent years, increasing attention has been paid to links between coexistence mechanisms and spatial patterns in plant communities (Pacala & Deutschman 1995; Tilman & Kareiva 1997; Murrell *et al.* 2001; Stoll & Prati 2001; Chesson & Neuhauser 2004). The primary objective of this analysis was to identify which descriptions of within- and between-species spatial structure were the most sensitive to coexistence mechanisms in a simulated plant community. The secondary objective was to fully describe the spatial signals of the modelled mechanisms.

The use of measures of spatial structure to quantify intraspecific aggregation and interspecific mingling is well established in both practical and theoretical research (e.g. Condit *et al.* 2000; Pommerening 2002; Souza & Martins 2003; Shimatani & Kubota 2004; Hao *et al.* 2007; Motz *et al.* 2010). However, the explanation of observed structure has long

been regarded as beyond the scope of these measures, not least because of the strong effects of dispersal limitation (Pacala & Levin 1997; Plotkin *et al.* 2000). Nevertheless, spatial statistics have been used to distinguish intra-specific and inter-specific associations (Roxburgh & Chesson 1998) and to link associations to competitive processes (Stoll & Prati 2001; Luo *et al.* 2012), to disentangle interspecific associations and environmental signals (Wiegand *et al.* 2007b) and to investigate the role of spatial structure in maintaining species richness and preventing competitive exclusion (Rácz & Karsai 2006; Damgaard 2010; Vogt *et al.* 2010; Luo *et al.* 2012).

We find that the measures considered here also give a clear and consistent description of spatial patterns under the different mechanisms that we model (Table 3). The niche mechanism produces communities composed of highly clustered and poorly mingled species, because of their association with particular geographically-defined habitats. The lottery (temporal niche) mechanism produces species with low levels of clumping and high levels of mingling, with considerable variation between species. Differences in the results of the spatial Simpson and ISAR indices suggest that common species (which were likely to have high fecundities at the time at which the simulations were stopped) were less mingled than rare species under the lottery mechanism. Communities generated under the assumptions of neutrality and heteromyopia had similar but more tightly constrained spatial properties in which both within- and between-species patterns were intermediate between those of the niche and Janzen-Connell mechanisms, although heteromyopia was found to increase intraspecific clumping and heterospecific mingling at very small scales, and to have effects that deviate markedly from neutrality as its strength increased (Fig. 6). This suggests that neighbouring heterospecifics had a tendency to be drawn from a smaller (proportional) pool of species under heteromyopia than under neutrality, perhaps because of the

formation of overlapping clumps of conspecifics. The Janzen-Connell mechanism, finally, produced widely distributed and uniformly mingled species, because of species' uniformly lower tolerances of high conspecific density.

The spatial statistics considered here make use of different pieces of information about spatial structure, and those that best captured differences between mechanisms - the measure of interspecific segregation and the proportion of conspecific neighbours for within-species structure, and the ISAR and spatial Simpson index for between species structure - are based on individual-level counts of conspecific and heterospecific neighbours. This information, when combined and averaged, therefore appears to be the most powerful discriminator between the effects of different modelled coexistence mechanisms (also, in the case of the spatial Simpson index, when combined with information from far larger scales). It is known that the identities of nearest neighbours can indicate ecological process (e.g. Pielou 1961; Wiegand *et al.* 2007b; Vogt *et al.* 2010), but links to particular mechanisms have not previously been investigated, with the exception of studies that indirectly use neighbour identities to search for evidence of density-dependence, Janzen-Connell mechanisms or effects of competition (e.g. Duncan 1991; Hubbell *et al.* 2001; Peters 2003; Uriarte *et al.* 2004). Nevertheless, we have shown that consistent spatial signals are detected at a range of strengths and combinations of mechanisms, and by a range of statistics, suggesting that these signals are direct spatial consequences of the mechanisms we modelled.

The combination of particularly informative spatial metrics and a principal components analysis of this combination reveal that the spatial Simpson index and proportion of conspecific neighbours together provide considerable discriminatory power when applied to

407 the mechanisms we modelled (a combination of statistics of this kind, based on different
408 aspects of spatial structure, is identified as valuable for detecting non-neutrality by May *et*
409 *al.* 2015 via a distinct approach). The spatial Simpson index provides most of the
410 information necessary to separate the niche-based and other mechanisms, while the
411 proportion of conspecific neighbours provides most of the information necessary to
412 separate the effects of spatial and temporal niches (Table S10, Fig. 7). This finding is
413 especially useful because it suggests an approach for empirical studies designed to
414 investigate mechanisms of these kinds. The measures require data only on nearest
415 neighbours and species abundances (with appropriate corrections for lack of observations
416 beyond study areas), and can easily be combined and focused on mechanisms of interest.

417 As the spatial patterns we identify follow from the modelled mechanisms in isolated and
418 combined form, and at a range of strengths, it can be expected that the measures will retain
419 some value in empirical settings where the effects of similar mechanisms are not entirely
420 confounded, especially for testing the highly divergent niche and neutral mechanisms (it is
421 important to note that the spatial signals of niche differentiation would vary with the scales
422 of environmental variation, niche sensitivity and analysis, as well as with the number of
423 environmental factors on which niche specialisation can occur). Previous studies support
424 this expectation, demonstrating the value of spatial statistics and associated predictions
425 developed in theoretical settings similar or identical to that used here (e.g. Wiegand &
426 Moloney 2004; Flügge *et al.* 2012; Brown *et al.* 2013; Damgaard *et al.* 2013). The inability of
427 theoretical simulations to establish any absolute statistical values indicative of processes in
428 real-world settings means that studies of relative values across sites may be most fruitful
429 (e.g. Baldeck *et al.* 2013). However, the differences identified here between the spatial
430 properties of individual species under different simulated mechanisms suggests that studies

within sites also hold promise, particularly for identifying species that may be strongly affected by a given mechanism (such as the Janzen-Connell effect, which is thought to vary substantially between species). In this context, an important - but unexplored - implication of our findings is that the variance of measures of spatial structure across scales could provide strong evidence of the occurrence and strength of species-specific mechanisms. None of this, of course, would allow the certain identification of any one underlying mechanism, especially given the potential strength of intra- and inter-specific variation in environmental responses and other relevant traits, but can be expected to be beneficial in eliminating possible causes of spatial structure, and hence species coexistence, that first-order or even single second-order statistics are unable to distinguish.

Acknowledgements

We thank Richard Law for his assistance with the research presented here. CB was partly funded by a Microsoft PhD Scholarship.

Data Accessibility

The model used here is freely available at:

https://bitbucket.org/cbrown23/plant-community-simulations-code

References

Anderson, M.J., et al. (2011) Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology letters* **14** (1), 19-28.

Baddeley, A. & Turner, R. (2005) SPATSTAT: an R package for the analyzing spatial point patterns. *Journal of Statistical Software* **12**, 1-42.

Baldeck, C. A., Harms, K. E., Yavitt, J. B., John, R., Turner, B. L., Valencia, R., … Dalling, J. W. (2013) Soil resources and topography shape local tree community structure in tropical forests. *Proceedings of the Royal Society B - Biological Sciences*, **280** (1753), 20122532.

Bar-Massada, A., Kent, R., & Carmel, Y. (2014). Environmental heterogeneity affects the location of modelled communities along the niche-neutrality continuum. *Proceedings of the Royal Society B - Biological Sciences*, **281**(1783), 20133249.

Beaudrot, L., Rejmánek, M., & Marshall, A.J. (2013). Dispersal modes affect tropical forest assembly across trophic levels. *Ecography* **36**(9), 984-993.

Bell, G. (2001) Neutral Macroecology. *Science*, **293** (5539), 2413-2418.

Brown, C., Law, R., Illian, J.B. & Burslem, D.F.R.P. (2011) Linking ecological processes with spatial and non-spatial patterns in plant communities. *Journal of Ecology*, **99** (6), 1402-1414.

Brown, C., Burslem, D. F. R. P., Illian, J. B., Bao, L., Brockelman, W., Cao, M., … Law, R. (2013). Multispecies coexistence of trees in tropical forests: spatial signals of topographic niche differentiation increase with environmental heterogeneity. *Proceedings of the Royal Society B - Biological Sciences*, **280**(1764), 20130502.

473 Chase, J. M. (2014). Spatial scale resolves the niche versus neutral theory debate. *Journal of*
474 *Vegetation Science*, **25**(2), 319–322.

475 Chave, J. (2004) Neutral theory and community ecology. *Ecology letters*, **7** (3), 241-253.

476 Chesson, P. & Neuhauser, C. (2004) Intraspecific aggregation and species coexistence. *Trends in*
477 *Ecology & Evolution*, **139** (3), 446-211.

478 Clark, D.A. & Clark, D.B. (1984) Spacing Dynamics of a Tropical Rain Forest Tree: Evaluation of the
479 Janzen-Connell Model. *The American Naturalist*, **124** (6), 769-788.

480 Clark, P.J. & Evans, F.C. (1954) Distance to Nearest Neighbor as a Measure of Spatial Relationships in
481 Populations. *Ecology*, **35** (4), 445-453.

482 Condit, R., Ashton, P.S., Baker, P., Bunyavejchewin, S., Gunatilleke, S., Gunatilleke, N., Hubbell, S.P.,
483 Foster, R.B., Itoh, A., LaFrankie, J.V., Lee, H.S., Losos, E., Manokaran, N., Sukumar, R. & Yamakura, T.
484 (2000) Spatial Patterns in the Distribution of Tropical Tree Species. *Science*, **288** (5470), 1414-1418.

485 Connell, J.H. (1970) On the role of natural enemies in preventing competitive exclusion in some
486 marine animals and in rainforest trees in Dynamics of populations, eds. P.J. den Boer & G.R.
487 Gradwell, PUDOC, Wageningen, 298-312.

488 Coomes, D.A., Rees, M. & Turnbull, L. (1999) Identifying Aggregation and Association in Fully
489 Mapped Spatial Data, *Ecology*, **80** (2), 554-565.

490 Dale, M.R.T., Dixon, P., Fortin, M., Legendre, P., Myers, D.E. & Rosenberg, M.S. (2002) Conceptual
491 and mathematical relationships among methods for spatial analysis. *Ecography*, **25** (5), 558-577.

492 Damgaard, C. (2010) Intraspecific aggregation does not increase species richness in dune grasslands.
493 *Journal of Ecology* **98** (5), 1141-1146.

494 Damgaard, C., Ejrnaes, R., Stevens, C.J. (2013). Intra-specific spatial aggregation in acidic grasslands:
495 effects of acidification and nitrogen deposition on spatial patterns of plant communities. *Journal of*
496 *Vegetation Science* **24**, 25-32.

497 Dixon, P. (1994) Testing Spatial Segregation Using a Nearest-Neighbor Contingency Table. *Ecology*,
498 **75** (7), 1940-1948.

499 Duncan, R.P. (1991) Competition and the Coexistence of Species in a Mixed Podocarp Stand. *Journal*
500 *of Ecology* **79** (4), 1073-1084.

501 Flügge, A.J., Olhede, S.C., Murrell, D.J. (2012). The memory of spatial patterns: changes in local
502 abundance and aggregation in a tropical forest. *Ecology* **93** (7), 1540-1549.

503 Gonzalez-Caro, S., Umana, M. N., Alvarez, E., Stevenson, P. R., & Swenson, N. G. (2014) Phylogenetic
504 alpha and beta diversity in tropical tree assemblages along regional-scale environmental gradients in
505 northwest South America. *Journal of Plant Ecology*, **7**(2), 145–153.

506 Gravel, D., Canham, C.D., Beaudet, M., Messier, C. (2006). Reconciling niche and neutrality: the
507 continuum hypothesis. *Ecology Letters,* **9** (4), 399-409.

508 Grinnell, J. (1917) Field Tests of Theories Concerning Distributional Control. *The American Naturalist*,
509 **51** (602), 115.

510 Gueze, M., Paneque-Galvez, J., Luz, A. C., Pino, J., Orta-Martinez, M., Reyes-Garcia, V., & Macia, M. J.
511 (2013). Determinants of tree species turnover in a southern amazonian rain forest. *Journal of*
512 *Vegetation Science*, **24**(2), 284–295.

513 Hao, Z., Zhang, J., Song, B., Ye, J. & Li, B. (2007) Vertical structure and spatial associations of
514 dominant tree species in an old-growth temperate forest. *Forest Ecology and Management*, **252** (1–
515 3), 1-11.

516 Hardy, O.J. & Sonké, B. (2004) Spatial pattern analysis of tree species distribution in a tropical rain
517 forest of Cameroon: assessing the role of limited dispersal and niche differentiation. *Forest Ecology*
518 *and Management*, **197** (1-3), 191-202.

519 Hubbell, S.P. (2001) The unified neutral theory of biodiversity and biogeography, 1st edn, Princeton
520 University Press, Princeton, NJ.

521 Hubbell, S.P., Ahumada, J.A., Condit, R. & Foster, R.B. (2001) Local neighbourhood effects on long-
522 term survival of individual trees in a neotropical forest. *Ecological Research*, **16** (5), 859-875.

523 Hutchinson, G.E. (1958) Concluding remarks in Cold Spring Harbor Symposia on Quantitative Biology,
524 22, 415-427.

525 Illian, J.B., Penttinen, A., Stoyan, H. & Stoyan, D. (2008) Statistical analysis and modelling of spatial
526 point patterns, 1st edn, Wiley, Chichester.

527 Illian, J. B., Sørbye, S. H., & Rue, H. (2012). A toolbox for fitting complex spatial point process models
528 using integrated nested Laplace approximation (INLA). *The Annals of Applied Statistics*, **6**(4), 1499–
529 1530.

530 Jaccard, P. (1912) The distribution of the flora in the alpine zone 1, Blackwell Publishing Ltd.

531 Jalilian, A., Guan, Y., Waagepetersen, R. (2013) Decomposition of variance for spatial Cox Processes.
532 *Scandinavian Journal of Statistics*, **40** (1), 119-137.

533 Janzen, D.H. (1970) Herbivores and the number of tree species in tropical forests. *The American*
534 *Naturalist*, **104** (940), 501.

535 Kraan, C., Aarts, G., van, d.M. & Piersma, T. (2010) The role of environmental variables in structuring
536 landscape-scale species distributions in seafloor habitats. *Ecology*, **91** (6), 1583-1590.

Law, R., Illian, J.B., Burslem, D.F.R.P., Gratzer, G., Gunatilleke, C.V.S. & Gunatilleke, I.A.U.N. (2009) Ecological information from spatial patterns of plants: insights from point process theory. *Journal of Ecology*, **97** (4), 616-628.

Legendre, P., Borcard, D. & Peres-Neto, P. (2005) Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecological Monographs*, **75** (4), 435-450.

Lin, Y., Chang, L., Yang, K., Wang, H. & Sun, I. (2011) Point patterns of tree distribution determined by habitat heterogeneity and dispersal limitation. *Oecologia*, **165** (1), 175-184.

Luo, Z.R., Yu, M.J., Chen, D.L., Wu, Y.G. & Ding, B.Y. (2012) Spatial associations of tree species in a subtropical evergreen broad-leaved forest. *Journal of Plant Ecology*, doi: 10.1093/jpe/rtr048

Martínez, I., Wiegand, T., González-Taboada, F. & Obeso, J.R. (2010) Spatial associations among tree species in a temperate forest community in North-western Spain. *Forest Ecology and Management*, **260** (4), 456-465.

Matérn, B. (1960) Spatial variation - lecture notes in statistics 36, Springer, Berlin.

May, F., Huth, A., & Wiegand, T. (2015). Moving beyond abundance distributions: neutral theory and spatial patterns in a tropical forest. *Proceedings of the Royal Society of London B: Biological Sciences*, *282*(1802), 20141657.

McGill, B.J., Etienne, R.S., Gray, J.S., Alonso, D., Anderson, M.J., Benecha, H.K., Dornelas, M., Enquist, B.J., Green, J.L., He, F., Hurlbert, A.H., Magurran, A.E., Marquet, P.A., Maurer, B.A., Ostling, A., Soykan, C.U., Ugland, K.I. & White, E.P. (2007) Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters*, **10** (10), 995-1015.

558 Mladenoff, D.J., White, M.A., Pastor, J. & Crow, T.R. (1993) Comparing Spatial Pattern in Unaltered
559 Old-Growth and Disturbed Forest Landscapes. *Ecological Applications*, **3** (2), 294-306.

560 Motz, K., Sterba, H. & Pommerening, A. (2010) Sampling measures of tree diversity. *Forest Ecology*
561 *and Management*, **260** (11), 1985-1996.

562 Münkemüller, T., de Bello, F., Meynard, C.N., Gravel, D., Lavergne, S., Mouillot, D., Mouquet, N. &
563 Thuiller, W. (2012) From diversity indices to community assembly processes: a test with simulated
564 data. *Ecography*, **35** (5), 468-480.

565 Murrell, D.J. & Law, R. (2003) Heteromyopia and the spatial coexistence of similar competitors.
566 *Ecology letters*, **6**, 48-59.

567 Murrell, D.J., Purves, D.W. & Law, R. (2001) Uniting pattern and process in plant ecology. *Trends in*
568 *Ecology & Evolution*, **16** (10), 529-530.

569 Odum, E.P. (1950) Bird Populations of the Highlands (North Carolina) Plateau in Relation to Plant
570 Succession and Avian Invasion. *Ecology*, **31** (4), 587-605.

571 Pacala, S.W. & Levin, S.A. (1997) Biologically generated spatial pattern and the coexistence of
572 competing species, in *Spatial Ecology*, eds. D. Tilman & P. Kareiva, Princeton University Press,
573 Princeton, 271-296.

574 Pacala, S.W. & Deutschman, D.H. (1995) Details That Matter: The Spatial Distribution of Individual
575 Trees Maintains Forest Ecosystem Function. *Oikos*, **74** (3), 357-365.

576 Packer, A. & Clay, K. (2000) Soil pathogens and spatial patterns of seedling mortality in a temperate
577 tree. *Nature*, **404**, 278-281.

578 Peters, H.A. (2003) Neighbour-regulated mortality: the influence of positive and negative density
579 dependence on tree populations in species-rich tropical forests. *Ecology Letters*, **6** (8), 757-765.

580 Pielou, E.C. (1961) Segregation and Symmetry in Two-Species Populations as Studied by Nearest-
581 Neighbour Relationships. *Journal of Ecology*, **49** (2), 255-269.

582 Plotkin, J.B., Potts, M.D., Leslie, N., Manokaran, N., Lafrankie, J. & Ashton, P.S. (2000) Species-area
583 Curves, Spatial Aggregation, and Habitat Specialization in Tropical Forests. *Journal of Theoretical*
584 *Biology*, **207** (1), 81-99.

585 Pommerening, A. (2002) Approaches to quantifying forest structures. *Forestry*, **75** (3), 305-324.

586 Rácz, É.V.P. & Karsai, J. (2006) **T**he effect of initial pattern on competitive exclusion. *Community*
587 *Ecology*, **7** (1), 23-33.

588 Rajala, T., & Illian, J. (2012). A family of spatial biodiversity measures based on graphs.
589 *Environmental and Ecological Statistics*, **19**(4), 545–572.

590 Rejmánek, M. (2002) Intraspecific aggregation and species coexistence. *Trends in Ecology &*
591 *Evolution*, **17** (5), 209-210.

592 Roxburgh, S.H. & Chesson, P. (1998) A New Method for Detecting Species Associations with Spatially
593 Autocorrelated Data. *Ecology*, **79** (6), 2180-2192.

594 Ruokolainen, L., Ranta, E., Kaitala, V. & Fowler, M.S. (2009) When can we distinguish between
595 neutral and non-neutral processes in community dynamics under ecological drift? *Ecology Letters*, **12**
596 (9), 909-919.

597 Salonen, V., Penttinen, A. & Särkka, A. (1992) Plant Colonization of a Bare Peat Surface: Population
598 Changes and Spatial Patterns. *Journal of Vegetation Science*, **3** (1), 113-118.

599 Seidler, T.G. & Plotkin, J.B. (2006) Seed dispersal and spatial pattern in tropical trees. *PLoS Biology*, **4**
600 (11).

601 Shimatani, K. (2001) Multivariate point processes and spatial variation of species diversity. *Forest*
602 *Ecology and Management*, **142** (1-3), 215-229.

603 Shimatani, K. & Kubota, Y. (2004) Quantitative assessment of multispecies spatial pattern with high
604 species diversity. *Ecological Research*, **19** (2), 149-163.

605 Smith, T.W. & Lundholm, J.T. (2010) Variation partitioning as a tool to distinguish between niche and
606 neutral processes. *Ecography*, **33** (4), 648-655.

607 Souza, A.F. & Martins, F.R. (2003) Spatial distribution of an undergrowth palm in fragments of the
608 Brazilian Atlantic Forest. *Plant Ecology*, **164** (2), 141-155.

609 Stoll, P. & Prati, D. (2001) Intraspecific Aggregation Alters Competitive Interactions in Experimental
610 Plant Communities. *Ecology*, **82** (2), 319-327.

611 Stoyan, D. & Penttinen, A. (2000) Recent Applications of Point Process Methods in Forestry Statistics.
612 *Statistical Science*, **15** (1), 61-78.

613 Tang, J. & Zhou, S. (2011) The importance of niche differentiation for coexistence on large scales.
614 *Journal of Theoretical Biology*, **273** (1), 32-36.

615 Tilman, D. & Kareiva, P. (eds) (1997) Spatial ecology - the role of space in population dynamics and
616 interspecific interactions, Princeton University Press, Princeton, New Jersey.

617 Tuomisto, H. (2010) A diversity of beta diversities: straightening up a concept gone awry. Part 2.
618 Quantifying beta diversity and related phenomena. *Ecography*, **33** (1), 23-45.

619 Uriarte, M., Condit, R., Canham, C.D. & Hubbell, S.P. (2004) A spatially explicit model of sapling
620 growth in a tropical forest: does the identity of neighbours matter? *Journal of Ecology*, **92** (2), 348-
621 360).

622 Vogt, D., Murrell, D. & Stoll, P. (2010) Testing Spatial Theories of Plant Coexistence: No Consistent
623 Differences in Intra- and Interspecific Interaction Distances. *The American Naturalist*, **175** (1), 73-84.

624 Wang, X., Wiegand, T., Hao, Z., Li, B., Ye, J. & Lin, F. (2010) Species associations in an old growth
625 temperate forest in north-eastern china. *Journal of Ecology*, **98**, 674-686.

626 Wang, X., Wiegand, T., Wolf, A., Howe, R., Davies, S.J. & Hao, Z. (2011) Spatial patterns of tree
627 species richness in two temperate forests. *Journal of Ecology*, **99** (6), 1382-1393.

628 Watt, A.S. (1947) Pattern and Process in the Plant Community. *Journal of Ecology*, **35** (1/2), 1-22.

629 Wiegand, T., Gunatilleke, C.V.S., Gunatilleke, I.A.U.N. & Huth, A. (2007a) How individual species
630 structure diversity in tropical forests. *Proceedings of the National Academy of Sciences*, **104** (48),
631 19029-19033.

632 Wiegand, T., Gunatilleke, S. & Gunatilleke, S. (2007b) Species associations in a hetergeneous Sri
633 Lankan dipterocarp forest. *The American naturalist*, **170** (4), E77-E95.

634 Wiegand, T. & A. Moloney, K. (2004) Rings, circles, and null-models for point pattern analysis in
635 ecology. *Oikos*, **104** (2), 209-229.

636 Wiegand, T. & Moloney, K.A. (2014) A handbook of spatial point pattern analysis in ecology.
637 Chapman and Hall/CRC press, Boca Raton, FL.

638 Wiegand, T., He, F., & Hubbell, S. P. (2013). A systematic comparison of summary characteristics for
639 quantifying point patterns in ecology. *Ecography*,*36*(1), 92-103.

Wright, S.J. (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia*, **130**, 1-14.

Zhang, J., Song, B., Li, B., Ye, J., Wang, X. & Hao, Z. (2010) Spatial patterns and associations of six congeneric species in an old-growth temperate forest. *Acta Oecologica*, **36** (1), 29-38.

Tables

Table 1: Separate pieces of information used in the spatial statistics considered here, and the symbols used to represent them.

Symbol	Meaning
n_j	number of individuals belonging to species *j* per unit area
n_k	number of individuals belonging to species *k* per unit area
n_i	number of individuals not belonging to species *j* per unit area
N_j	number of individuals belonging to species *j*
N_T	total number of individuals
N_c	number of individuals with a conspecific nearest neighbour
N_h	number of individuals with a heterospecific nearest neighbour
$N(r)$	number of neighbours within a defined radius *r*
$N_{jj}(r)$	number of conspecifics within a defined radius *r*
$N_{ij}(r)$	number of heterospecifics within a defined radius *r*
$N_{jk}(r)$	number of pairs of individuals belonging to species *j* and *k* within a defined radius *r* of one another
$N_{jk}(\check{r})$	number of pairs of individuals belonging to species *j* and *k* separated by distance *r* (in practice, within range ($r + dr$)
$N_s(r)$	number of species within a defined radius *r*
N_s	total number of species
P_j	proportion of community represented by species *j*
A_c	area considered in count of points; area of circle to radius *r*, or of annulus within ($r + dr$), as appropriate
A_{jk}	area under the pair correlation function of species *j* and *k*
R	radius limit to which a calculation is made

Table 2: Definitions of statistics measuring spatial structure. Individual terms are explained in Table 1, and alternative definitions in terms of spatial point process functions are given in Table S4. No edge correction was used because statistics were calculated from simulated communities projected on a torus, but such correction would be necessary for real-world data. Statistics are expressed here at the species level, with the exception of the spatial Simpson index which is only calculated at community level. Species-level statistics are subsequently averaged across species to community level (with the ISAR additionally normalised for species richness). Equations for this averaging are given in Table S5.

Name	**Definition**	**Source**
Degree of aggregation	$D_{ag}(r) = \sum_1^{N_j} \frac{N_{jj}(r)}{\pi r^2 n_j(1-n_j)}$	Coomes *et al*. (1999)
Measure of interspecific segregation	$S_j = log\left[\frac{N_c/N_h}{(n_j-1)/n_i}\right]$	Dixon (1994)
Proportion of conspecific neighbours	$P_c = \frac{N_{jj}(r)}{N(r)}$	
ISAR	ISAR$_j$(*r*) = $\overline{N}_s(r)$	Wiegand *et al.* (2007a)
Spatial Simpson index (cumulative)	$S(r) = 1 - \sum_{j=1}^{N_s} P_j \frac{\overline{N_{jj}}(r)}{\bar{N}(r)}$	Shimatani (2001); Rajala & Illian (2012)
Degree of association	$D_{as}(r) = \sum_1^{N_j} \frac{N_{jk}(r)}{n_i n_k A_c}$	Coomes *et al*. (1999)
Cross-pair overlap distribution	$xPOD(R) = \left\{A_{jk} = \int_0^R \log\left(\frac{N_{jk}(\check{r})}{n_j n_k A_c}\right) dr \,; j,k = 1{:}N_s \,, j \neq k\right\}$	Brown *et al.* (2011)

722

723

Table 3: Principal characteristics of spatial patterns generated under each modelled mechanism in terms of scattering, exposure, and implications for turnover of species with distance (Beta-diversity). Results are expressed relative to the neutral case, which has intermediate levels of scattering, exposure and turnover due to density-dependent mortality and dispersal limitation.

724

	Janzen-Connell	**Neutral**	**Heteromyopia**	**Niche**	**Lottery**
Scattering	High; highly consistent across species		Low at very small scales but higher at intermediate scales	Very low; consistent across species	High but variable; some species strongly aggregated, others strongly scattered
Exposure	High; highly consistent across species		At small scales, exposure between heterospecifics is elevated but exposure between species is depressed. Both increase towards intermediate scales but become neutral as scale increases further.	Low at small scales but high at intermediate-large scales	High on average but low in the most abundant species
Beta-diversity (turnover)	Rapid rate of turnover with distance		Rapid at small scales, neutral at larger scales	Rate of turnover similar to neutral	Highly variable

725

726

727

728

729

Figures

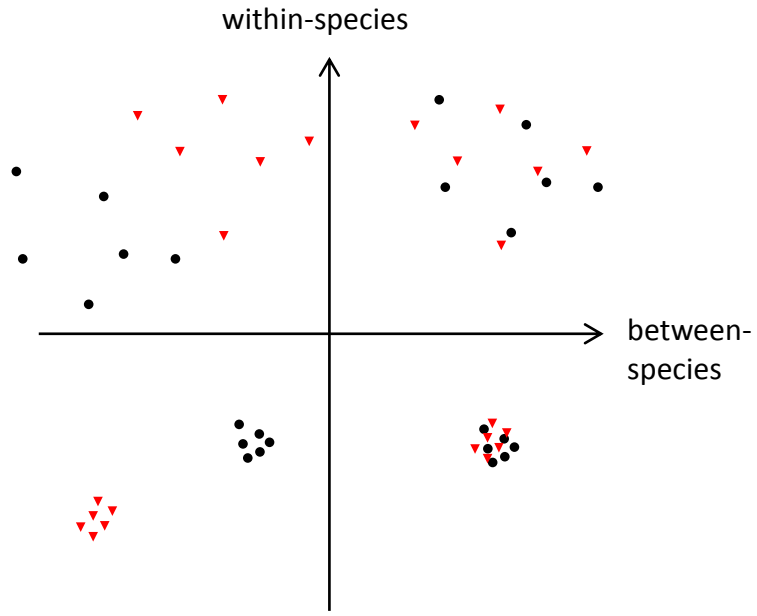


Figure 1: Extremes of within- and between-species spatial structure. Within-species structure varies between clustering and regularity, between-species structure between mingling and segregation

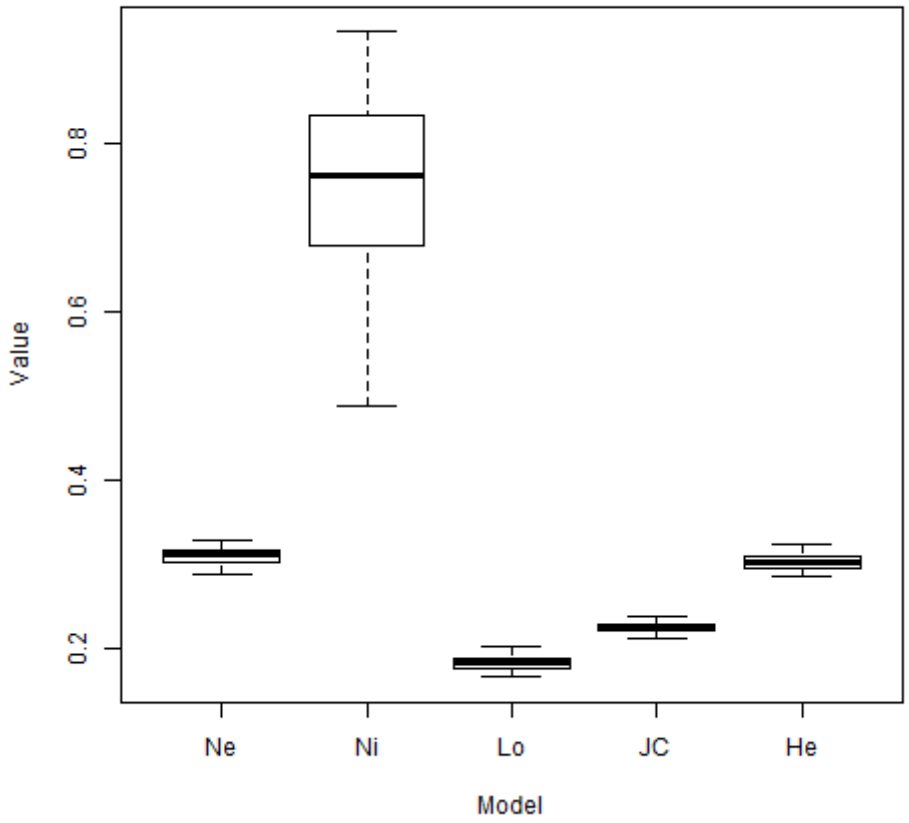
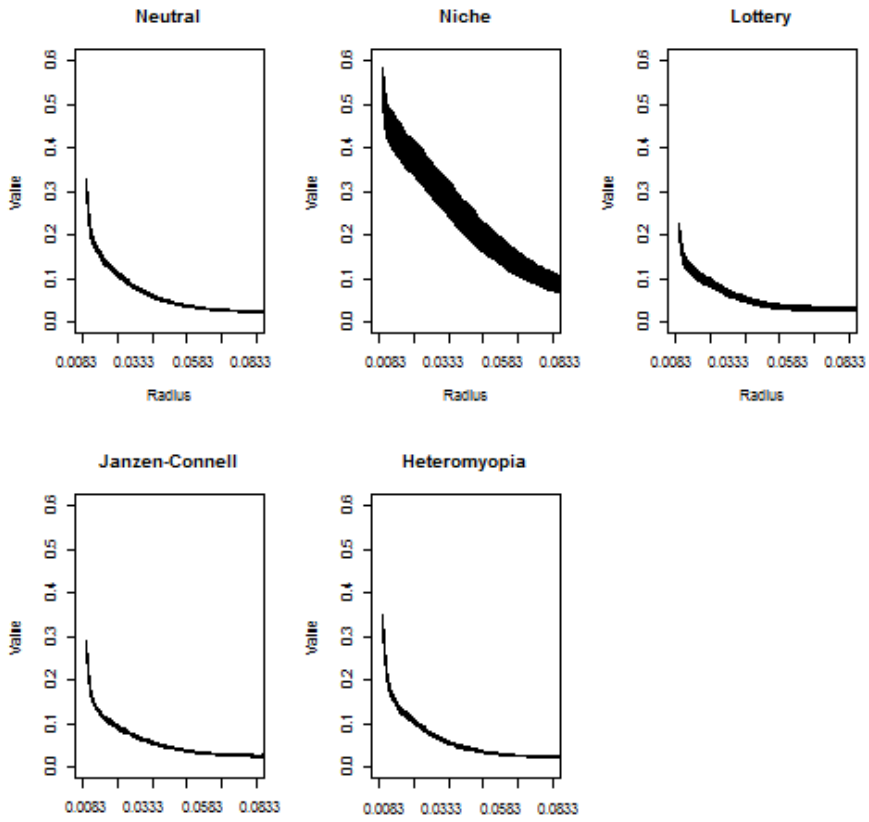


Figure 2: The measure of interspecific segregation across 30 realisations of each modelled mechanism (each realisation contributes one (community-level) value of the index). Abbreviations are as follows: Ne = Neutral; Ni = Niche; Lo = Lottery; JC = Janzen-Connell; He = Heteromyopia.

(a)



(b)

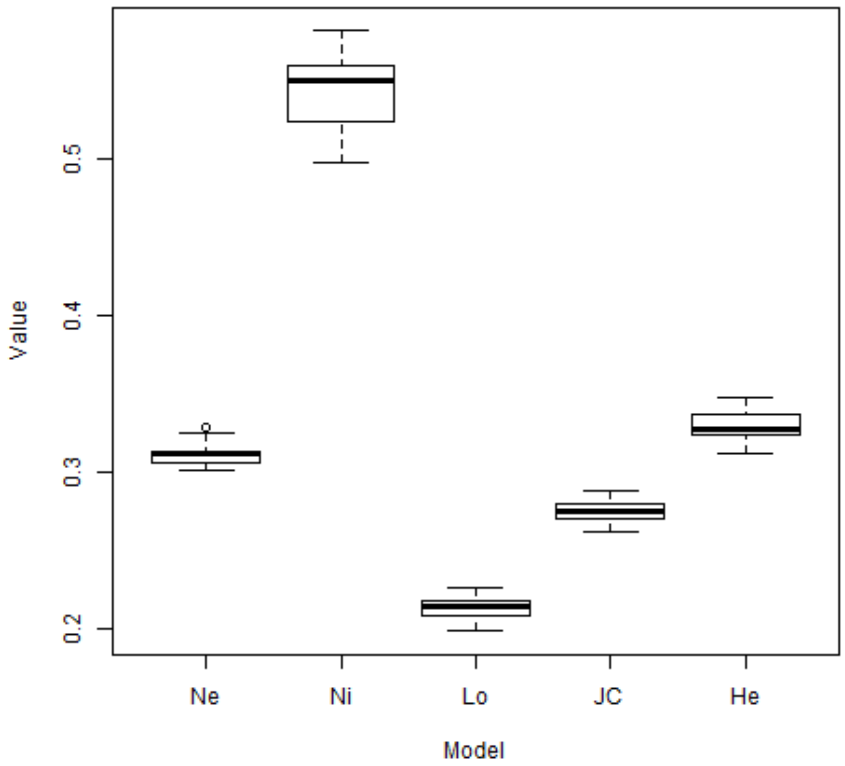


Figure 3: The proportion of conspecific neighbours across 30 realisations of each modelled mechanism, across radii (a) and at a radius of 0.0025 (b). Abbreviations are as follows: Ne = Neutral; Ni = Niche; Lo = Lottery; JC = Janzen-Connell; He = Heteromyopia.

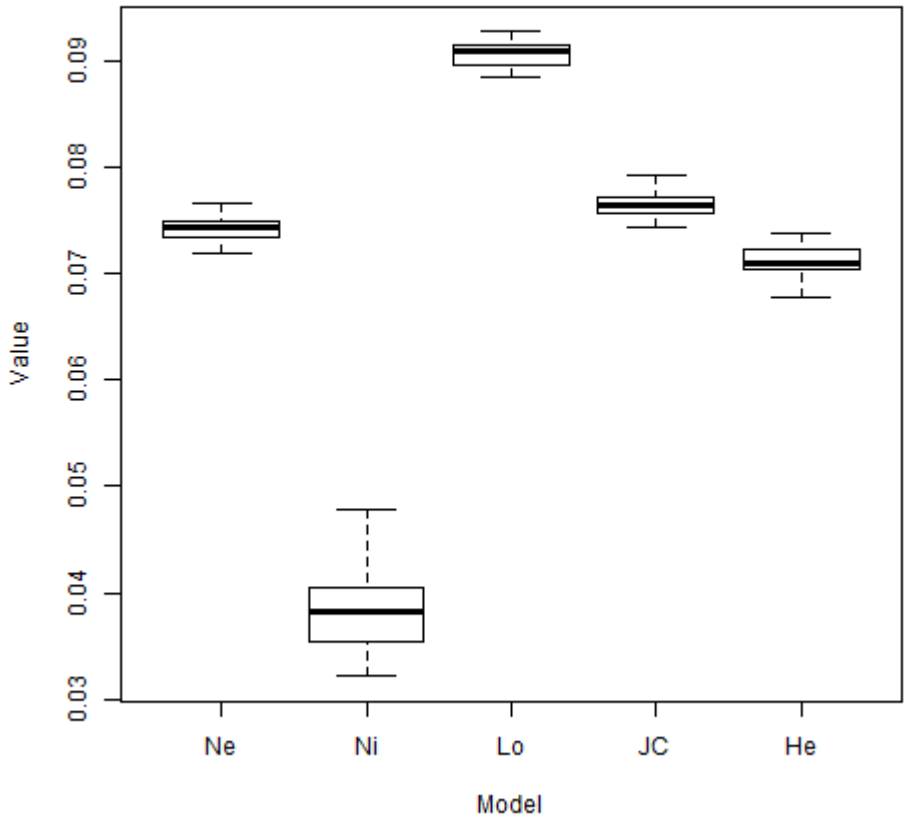


Figure 4: The normalised community-level individual species-area relationship (ISAR) across 30 realisations of each modelled mechanism, at a radius of 0.0083 (expressed as a proportion of the total number of species within each simulated community). Abbreviations are as follows: Ne = Neutral; Ni = Niche; Lo = Lottery; JC = Janzen-Connell; He = Heteromyopia.

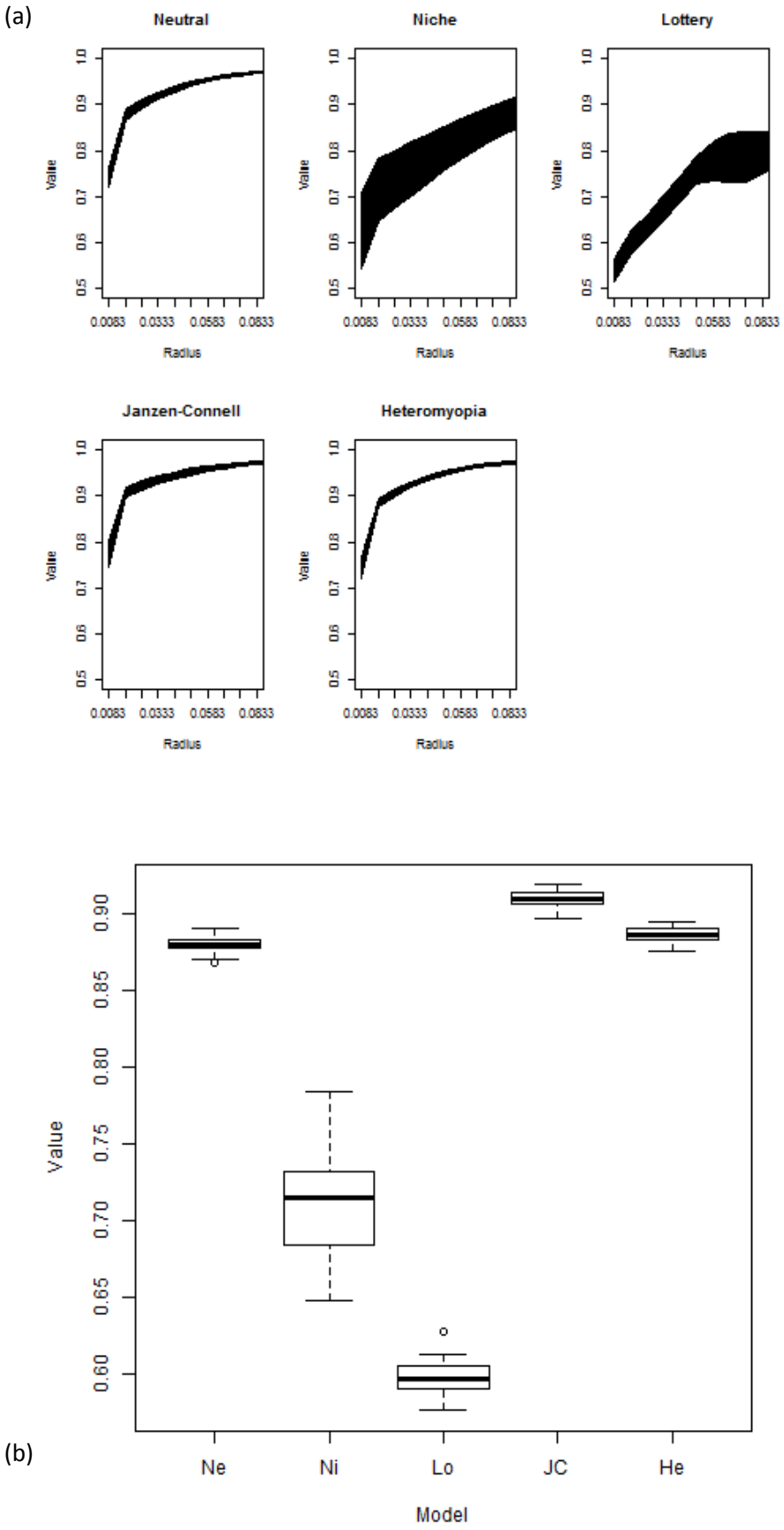
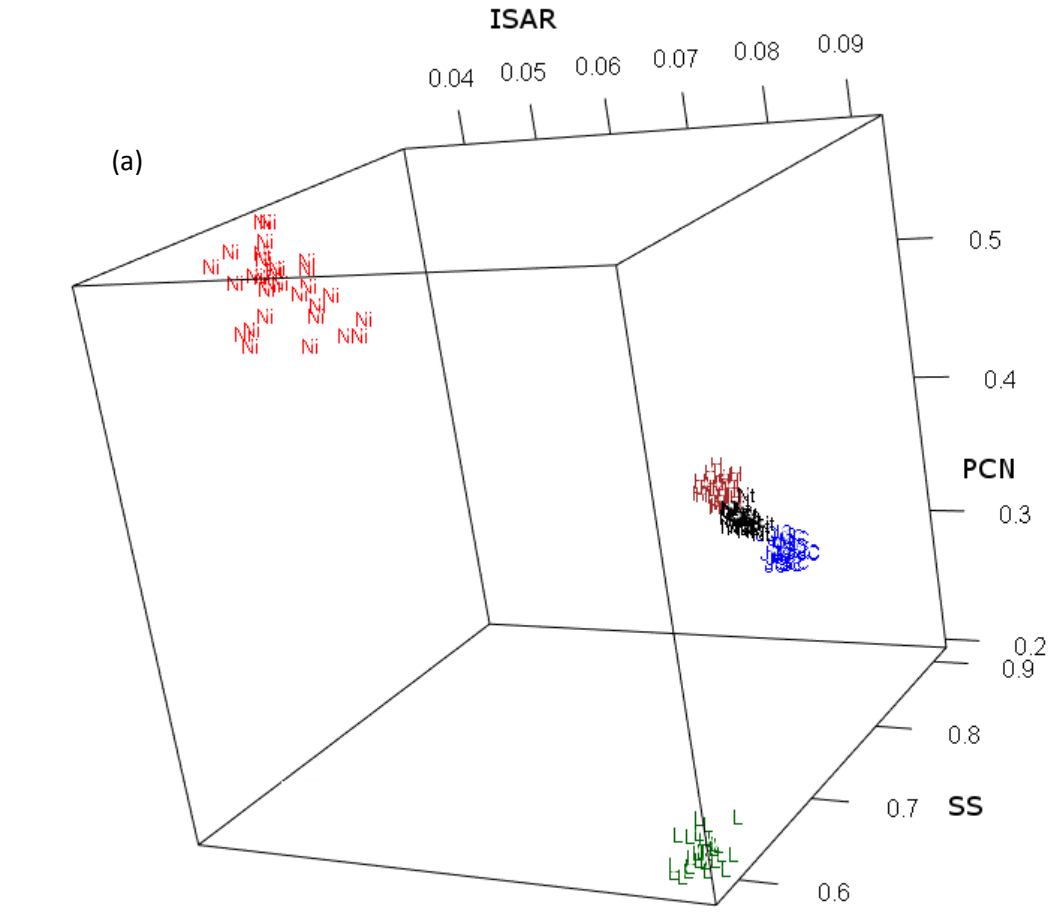
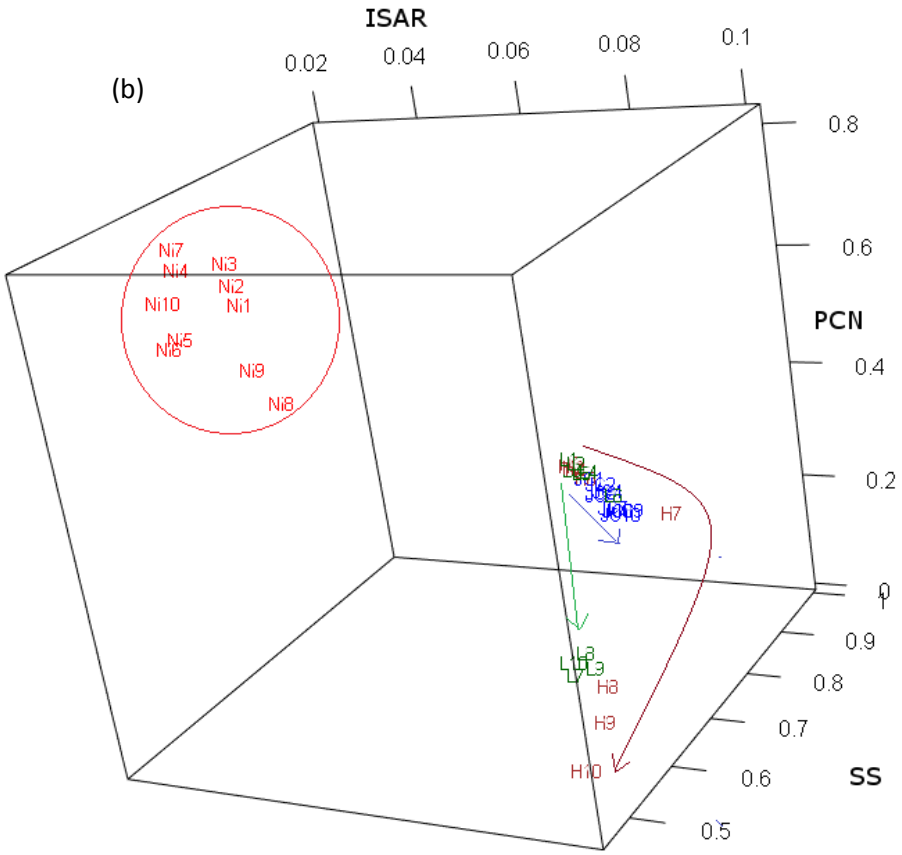


Figure 5: The spatial Simpson index across 30 realisations of each modelled mechanism, across radii (a) and at a radius of 0.0083 (b). Abbreviations are as follows: Ne = Neutral; Ni = Niche; Lo = Lottery; JC = Janzen-Connell; He = Heteromyopia.


(a)
ISAR
0.04
0.05
0.06
0.07
0.08
0.09
PCN
0.5
0.4
0.3
0.2
SS
0.9
0.8
0.7
0.6


(b)
ISAR
0.02
0.04
0.06
0.08
0.1
PCN
0.8
0.6
0.4
0.2
0
SS
0.9
0.8
0.7
0.6
0.5
Ni7
Ni4
Ni3
Ni2
Ni10
Ni1
Ni5
Ni6
Ni9
Ni8
H7
H8
H9
H10

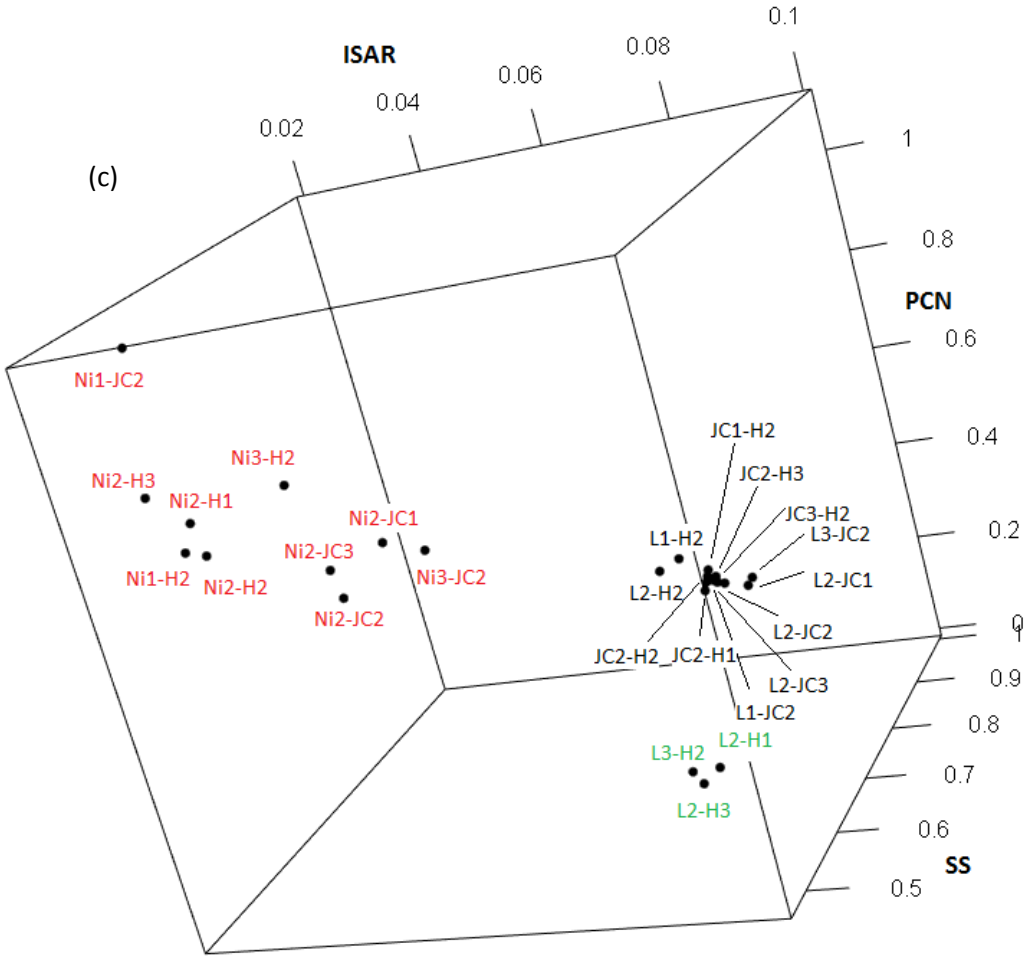


Figure 6: Values taken by each of the original 30 simulations of each modelled mechanism (a), the additional 10 simulations of each in the sensitivity analysis (b), and the 25 simulations of combined mechanisms at a range of strengths (c). Results are presented for a combination of the normalised individual species area relationship (ISAR), spatial Simpson index (SS) and proportion of conspecific neighbours (PCN), calculated at the community level and at radii of 0.0083, 0.0167 and 0.0025 of plot dimension respectively. Individual simulations of each mechanism are labelled 1-10 in (b), with 1 corresponding to the weakest modelled strength of the mechanism and 10 the strongest (see Table S2). Arrows indicate direction of movement where results move in a consistent direction in statistical space with increasing strength of the modelled mechanism; results are circled otherwise. In (c), individual simulations are labelled by the two mechanisms used in each, along with a number (1-3) indicating the strength of each mechanism, from the three strengths given in Table S3 (1=lowest strength, 3 = highest strength). Mechanisms are abbreviated as: Nt = Neutral (black), Ni = Niche (red), JC = Janzen-Connell (blue), H = heteromyopia (brown), L = lottery (green).

937

938

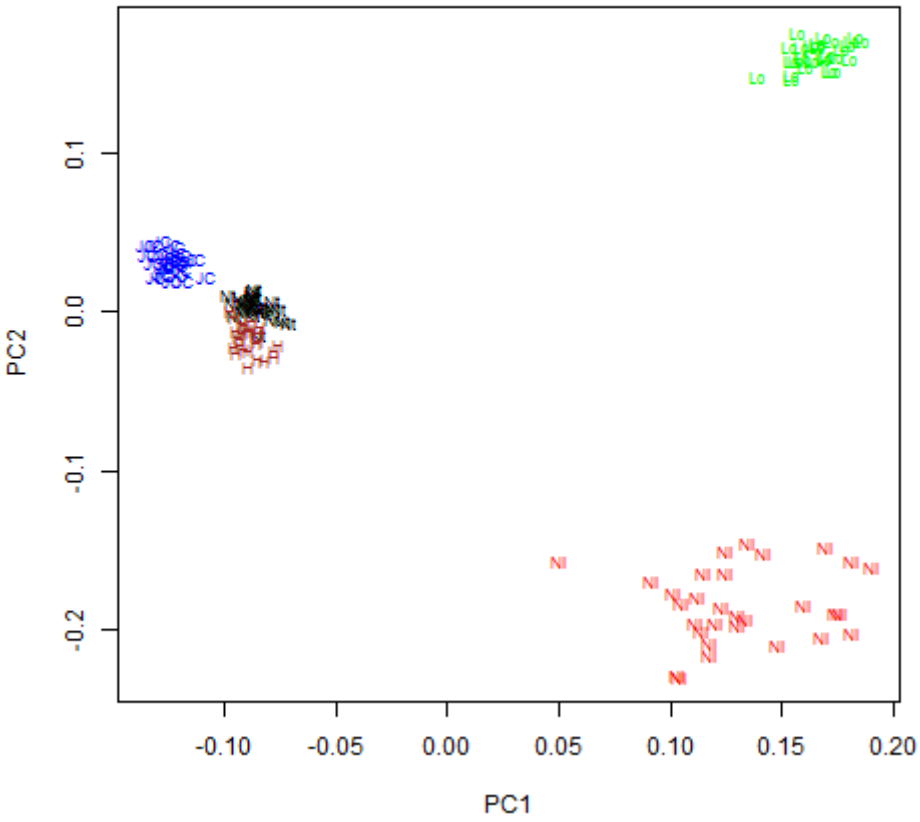


Figure 7: Results of a principal components analysis of the values plotted in Figure 6a. The positions of each of the 30 simulations of each modelled mechanism on the first two principal components are shown; these components are explained in Table S10. Mechanisms are abbreviated as: Nt = Neutral (black), Ni = Niche (red), JC = Janzen-Connell (blue), H = heteromyopia (brown), L = lottery (green).